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Interspecific competition counteracts negative effects of dispersal on adaptation of an arthropod herbivore to a new host

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dispersal;
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interspecific competition;
local adaptation;
spider mites.

Abstract

Dispersal and competition have both been suggested to drive variation in adaptability to a new environment, either positively or negatively. A simultaneous experimental test of both mechanisms is however lacking. Here, we experimentally investigate how population dynamics and local adaptation to a new host plant in a model species, the two-spotted spider mite (*Tetranychus urticae*), are affected by dispersal from a stock population (no-adapted) and competition with an already adapted spider mite species (*Tetranychus evansi*). For the population dynamics, we find that competition generally reduces population size and increases the risk of population extinction. However, these negative effects are counteracted by dispersal. For local adaptation, the roles of competition and dispersal are reversed. Without competition, dispersal exerts a negative effect on adaptation (measured as fecundity) to a novel host and females receiving the highest number of immigrants performed similarly to the stock population females. By contrast, with competition, adding more immigrants did not result in a lower fecundity. Females from populations with competition receiving the highest number of immigrants had a significantly higher fecundity than females from populations without competition (same dispersal treatment) and than the stock population females. We suggest that by exerting a stronger selection on the adapting populations, competition can counteract the migration load effect of dispersal. Interestingly, adaptation to the new host does not significantly reduce performance on the ancestral host, regardless of dispersal rate or competition. Our results highlight that assessments of how species can adapt to changing conditions need to jointly consider connectivity and the community context.

Introduction

The capacity to adapt to novel habitats is essential for several evolutionary and ecological processes, such as niche and range shift or expansion (Holt & Gomulkiewicz, 1996; Kawecki & Ebert, 2004; Kawecki, 2008) and ultimately speciation. Dispersal and the community context are likely to influence the capacity to adapt to novel habitats (Kawecki, 2008). Dispersal is one of the

most important processes influencing adaptation dynamics (Holt & Gomulkiewicz, 1996). On the one hand, dispersal can have positive effects on adaptation by exerting a demographic and genetic (via gene flow) rescue effect, replenishing population density and genetic variation (Lenormand, 2012). This is particularly relevant to small (e.g. island) populations, and those inhabiting marginal habitats or at the edge of the species ranges (MacArthur & Wilson, 1967; Brown & Kondric-Brown, 1977). Dispersal can sustain these populations long enough to allow them to adapt to a new habitat (Kawecki, 1995; Holt & Gomulkiewicz, 1997). On the other hand, dispersal can hinder adaptation if the rate of immigration is high relative to selection and drift, that is migration load (Cuevas *et al.*, 2003; Bolnick

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& Nosil, 2007), or via an increased population size that exceeds the carrying capacity, producing a collapse of the population that cannot be sustained by its environment (Holt & Gomulkiewicz, 1997; Garant *et al.*, 2007). Although positive and negative effects of dispersal on local adaptation have been separately reported (reviewed in Garant *et al.*, 2007), only a handful of studies have shown that dispersal can exert both effects. Yeast adaptation to salt stress has been shown to be favoured by local dispersal and reduced by global dispersal (Bell & Gonzalez, 2011). Similarly, the relationship between dispersal and adaptation in bacteriophages is best described by an upward concave curve with intermediate levels of dispersal maximizing adaptation (Ching *et al.*, 2012). Whether this pattern is also present in more complex organisms still needs experimental demonstration.

In addition to dispersal, the community context might influence rates of local adaptation. Traditionally, studies of local adaptation have considered a single species responding to a novel environment (Johansson, 2007). However, species generally co-occur with many others, and the eco-evolutionary dynamics resulting from these complex interactions might diverge from the ones predicted by single species approaches (Johansson, 2007; De Mazancourt *et al.*, 2008; Urban *et al.*, 2011; Lawrence *et al.*, 2012; De Meester *et al.*, 2016). Theoretical studies have shown that competition can affect adaptation, either negatively or positively, depending on the specific conditions of the system (Johansson, 2007; Osmond & de Mazancourt, 2013). For instance, competition is known to decrease population abundances and increase extinction risk (Gause & Witt, 1935; Bengtsson, 1989; Johansson, 2007; De Mazancourt *et al.*, 2008). Competition can also constrain evolutionary rescue (Osmond & de Mazancourt, 2013) and can keep populations away from the fitness local optima by reducing selection pressure for tracking changes in the environment (Johansson, 2007). While most of the theoretical studies have shown that competition can hinder adaptation (reviewed in Urban *et al.*, 2011), some studies have shown that adaptation can be favoured by interspecific competition (Jones, 2008; Osmond & de Mazancourt, 2013), as it increases selection pressure to speed up the adaptation process or it can promote resource partitioning and character displacement (Stuart *et al.*, 2014). However, experimental evidence of the effect of competition on local adaptation is still scarce.

Here, using experimental evolution, we studied the effects of dispersal and interspecific competition on local adaptation. We allowed 56 experimental populations of the two-spotted spider mite (*Tetranychus urticae*) to adapt to a new, challenging host (tomato plants, *Solanum lycopersicum*) under different scenarios of dispersal and competition. Populations varied in the number of immigrants coming from the population kept in

the ancestral host plant (from here onwards stock population) and in the co-occurrence with a closely related species (*Tetranychus evansi*) that is specialized on the plant family Solanaceae to which the tomato plant belongs. We measured the level of adaptation of each population to the new host plant after eight and 20 generations of the evolutionary experiment using fitness tests and compared this with the performance of the stock population. Our results show that dispersal has a negative effect on adaptation to a new host plant for populations that do not experience interspecific competition, but that such competition counteracts these negative effects, allowing populations to adapt even at high levels of immigration.

Materials and methods

Study species

The two-spotted spider mite *T. urticae* Koch, 1836 (Acari, Tetranychidae), is a cosmopolitan generalist herbivore that uses a wide range of host plants, feeding on more than 900 plant species and 124 plant families (Gotoh *et al.*, 1993; Bolland *et al.*, 1998). *Tetranychus urticae* is considered an ideal model for mesocosm experiments on adaptation (Gould, 1979; Fry, 1990; Agrawal, 2000; Egas & Sabelis, 2001; Magalhaes *et al.*, 2007; Kant *et al.*, 2008; Bonte *et al.*, 2010). The arguments include well-known biology and genomics (Grbić *et al.*, 2011), small body size (female size about 0.4 mm length), high fecundity (1–12 eggs per day) and short generation time, ranging from 11 to 28 days depending on the environmental conditions (Nacimiento de Vasconcelos *et al.*, 2008).

Competitor species

Because all closely related competitors can exert indirect plant-mediated effects on *T. urticae* (Kant *et al.*, 2004, 2008; Sarmiento *et al.*, 2011a; Godinho *et al.*, 2015), we chose one that is known for a strong net negative effect (Sarmiento *et al.*, 2011b); the red spider mite *T. evansi* Baker and Pritchard, 1960. This species is mainly a specialist herbivore of Solanaceae and is considered an important agricultural pest. Its body size ranges from 0.5 to 0.6 mm (adult female), fecundity ranges from 10 to 14 eggs per day (Navajas *et al.*, 2013) and development time can vary from 6.3 to 13.5 days, depending on the environmental temperature and host (Bonato, 1999).

Experimental evolution

We used a mesocosm experiment to test the effects of dispersal and interspecific competition on adaptation to a new host plant. We initiated experimental populations on single tomato plants (4 weeks old, *Solanum*

lycopersicum variety 'money maker') from three individual adult females coming from a population of *T. urticae* adapted to bean plants (stock population). This population (London strain) was originally collected from the vineland region in Ontario, Canada (Grbić *et al.*, 2011), and has a high standing genetic variation for adaptation towards novel host plants (e.g. Wybouw *et al.*, 2015). This stock population was maintained on bean plants (*Phaseolus vulgaris* variety prelude) for more than 5 years (pers. comm. Thomas Van Leeuwen). To assess the effect of dispersal (the immigration rate), we introduced individual females from the stock to the experimental populations. This experimental system thus reflects a mainland-island system with highly directional gene flow towards the novel islands. We used four levels of dispersal rate: two, three, five and 10 adult female mites per week. To assess the effect of competition, we seeded, only at the beginning of the experiment, half of the experimental plants with three individuals of *T. evansi* 3 days before the first immigration event of *T. urticae*. Individuals of both species are easily distinguishable. Individuals of *T. evansi* show a characteristic red coloration, whereas individuals of *T. urticae* are pale with two black dots on their backs. *T. evansi* did not need to be replenished as it always maintained high population sizes being adapted to tomato plants. We used seven replicates each per dispersal-competition treatment combination for a total of 56 (four dispersal levels \times two competition treatments \times seven replicates) experimental units. To avoid mite dispersal among the different experimental units, we used yellow sticky traps (Pherobank) to cover the floor where plants were placed. The experimental units (tomato plants with mite populations) were kept in a climate control room at $25 \pm 0.5^\circ\text{C}$ with a 16–8 h light/dark regime. Plants from each experimental unit were refreshed every two weeks because of mite consumption, by transferring all leaves and stems with mites from the old tomato plant to a new tomato plant. The experiment was performed for 20 generations, over a seven-month period.

We monitored the populations (number of adult females) during the evolutionary experiment one day before the weekly dispersal routine. We studied the effect of competition and dispersal on the size of these populations for generations 9 and 12. To study the effect on population survival, we recorded the number of extinction events during 161 days of the experiment (until generation 12) and recorded the proportion of extinct populations at generation 20.

To assess how dispersal and interspecific competition affect the level of adaptation, we performed fitness tests at generations 8 and 20. Studies on the same species have shown a response to selection after five generations (Agrawal, 2000) and an adaptation plateau at 15 generations (Magalhaes *et al.*, 2009). Samples (1–5 adult females depending on population sizes on plants) from each experimental unit were collected to start

iso-female lines. Each female was reared separately on a bean leaf disc (a 4×5 cm leaf disc placed on distilled-water soaked cotton, common garden) for two generations to remove juvenile and maternal effects (Magalhaes *et al.*, 2011; Kawecki *et al.*, 2012). From each iso-female line, two daughters were used for testing their level of adaptation using two fitness proxies (fecundity and longevity), on bean and tomato leaf discs (2×3 cm). Pictures were taken daily during 15 days for subsequent analyses. To quantify fitness, we recorded total fecundity and female longevity from photographs. Total fecundity (number of eggs) was measured at day 6. Females that had drowned in wet cotton or disappeared before day 6 were excluded. Female longevity was measured as the number of days that a female was alive. At generation 8, we did not perform fitness tests using populations under competition because of their low population size.

To test whether long-term (rather than short-term) adaptation to tomato is necessary to detect a cost of adaptation on the ancestral host, we compared the fecundity on tomato and bean plants of a tomato-adapted London-strain population (which is the same original strain as the stock population, but reared on tomato instead of bean for more than 100 generations) against the performance of the stock population. Females from both populations were collected and individually placed on bean leaf discs to start iso-female lines. Females remained on bean leaf discs for two generations to remove epigenetic effects before performing fitness tests. From each iso-female line, two females were collected and each one was placed on either bean or tomato leaf discs. Fecundity of each female was recorded from daily photographs.

Data analysis

Adaptation to tomato (fitness tests after removal of juvenile and maternal effects)

Effect of dispersal and competition. We tested the effect of dispersal and competition on adaptation (fecundity) to tomato plants using generalized linear mixed models (GLMMs) with a Poisson error distribution. This analysis was only possible after 20 generations of the evolutionary experiment, because populations under competition were not large enough after eight generations. The full factorial model included two fixed factors: competition treatment with two levels (competition and no competition) and dispersal with four levels (2, 3, 5 and 10 mites per week). Replicate was included as a random factor. For model selection, we performed a stepwise removal of non-significant fixed effects from the full model, and tested the effect of removal with a log-likelihood ratio test. *Post hoc* comparisons were not possible due to low levels of replication in some treatments.

To maximize the use of the data available for populations without, we ran an additional GLMM model with a Poisson error distribution to test the effect of dispersal on adaptation to tomato (fecundity) for populations without competition after eight and 20 generations of the evolutionary experiment. The model included dispersal as a fixed factor with four levels (2, 3, 5 and 10 mites per week) and replicate as a random factor. Model selection was performed as before. Multiple comparison of means was performed using the Tukey's HSD test.

Adaptation and cost of adaptation to tomato. We study whether populations from different treatments show adaptation and/or cost of adaptation to tomato, that is loss of adaptation to the ancestral host (bean). We compared the fecundity on tomato (to test adaptation) and on bean (to test cost of adaptation) of each treatment against the fecundity on tomato and on bean of the stock population (population that has not been exposed to tomato plants) using a Tukey's HSD test. We performed the multiple comparison analysis for: (i) populations without competition after eight generations, (ii) populations without competition after 20 generations and (iii) populations under competition after 20 generations. Data after 20 generations were analysed separately for treatments with and without competition to be able to test all dispersal levels under no competition. Additionally, we compared adaptation levels (total fecundity) between the adapted population (> 100 generations on tomato) and the stock population using generalized linear mixed models (GLMMs) with replicate (each iso-female line per population) as a random factor and a Poisson error distribution.

Female longevity. The effects of dispersal on female longevity, for generations 8 and 20, were tested with survival analysis using cox proportional hazard mixed effects models. Testing the combined effect of dispersal and competition was only possible for generation 20. In this model, we considered dispersal (four levels), treatment (two levels, only for generation 20) and plant species (two levels) as fixed factors and iso-female lines nested in replicates as random factors. Females that were alive at the end of the experiment or had died from non-natural causes, for example drowning, were considered as censored data. We ran an additional model only using the data of the no-competition treatments. This model considered dispersal (four levels), plant species (two levels) and generation (two levels) as fixed factors and replicate as a random factor. Again, model selection was carried out by removing nonsignificant fixed effects in a stepwise manner from the full model, and performing a log-likelihood ratio test.

Fecundity – longevity trade-offs. Trade-offs between female longevity (using noncensored data, that is the

real deaths, excluding females that drowned in the wet cotton or that survived until the end of the experiment) and total fecundity were assessed using linear mixed models for generations 8 and 20. Full models for both generations included dispersal, longevity and plant species as fixed factors and replicate as a random factor. Additionally, we included a nonlinear term (longevity^2) to test the quadratic relationship between longevity and dispersal. Full models for generation 20 also included competition as a fixed factor. Model selection was performed as before by removing nonsignificant fixed effects in a backward stepwise manner from the full model. We tested the effect of dropping factors based on a log-likelihood ratio test.

Adaptation to tomato in the experimental plants (before removal of juvenile and maternal effects)

For generations 9 and 12, we examined the effect of competition and dispersal on population size, on number of extinction events (the number of times in 12 generations that populations reach 0 adult females that is pseudo-extinction levels) and on population survival (whether each population survived after 20 generations on tomato). For each test, we used, respectively, linear models, linear models with Poisson error distribution and a logistic regression using generalized linear models with a binomial error distribution. Because distinguishing juvenile stages is not possible without a microscope, and a microscope cannot be used on complete plants, we used the number of adult females (which are big enough to be counted with the naked eye) as a proxy of the real population size, which can be 10–15 times higher (S2 in De Roissart *et al.*, 2015), present in the 56 experimental populations. Population size was log-transformed to meet normality of model residuals when necessary. Model selection was performed as before.

All analyses were performed with R version 3.0.1 and the R packages: lme4 version 1.1-10 (Bates *et al.*, 2015), nlme version 3.1-122 (Pinheiro *et al.*, 2015), MuMIn version 1.15.1 (Barton, 2015), survival version 2.38-3 (Therneau, 2015a), multcomp version 1.4-1 (Hothorn *et al.*, 2008), plotrix version 3.6 (Lemon, 2006) and Coxme version 2.2-4 (Therneau, 2015b).

Results

Adaptation to tomato in the fitness tests (after removal of juvenile and maternal effects)

Effects of dispersal and competition on fecundity

After eight generations, without competition, dispersal did not have an effect on adaptation to tomato plants (Table 1, Fig. 1a) and all populations show a similar fecundity to the stock population (Table 2). However, after 20 generations, and without competition, dispersal negatively affected adaptation to tomato plants (Table 1, Fig. 1b). Populations receiving the highest

level of dispersal showed on average significantly lower fecundity (3.35 ± 1.65) than populations receiving the lowest dispersal level (19.69 ± 1.82).

These patterns were however different under competition, as indicated by the significant interaction term (Table 1): populations with competition for the highest dispersal level (10 mites per week) have on average a significantly higher fecundity (17.29 ± 1.88) than populations without competition (3.35 ± 1.65). For model selection, see Table S1.

Adaptation and cost of adaptation to tomato plants

A comparison of the fecundity between populations without competition and the stock population shows that only the population receiving the highest level of dispersal had not significantly adapted to tomato plants (Table 2), whereas the rest of the populations have on average significantly higher fecundity than the stock population (Table 2). Comparison of the fecundity of populations with competition to the stock population shows significantly higher fecundity for the population under competition than for the stock population for all dispersal levels where we had enough females to perform a proper test (Table 2).

Female mites did not show a significant cost of adaptation neither after eight or 20 generations of selection on tomato plants (Table 2, Fig. 1d, e). Female fecundity on bean leaves was similarly high to the one of the stock population (adapted to bean plants). A cost of adaptation was not even detected after long-term adaptation to tomato plants. Females from the tomato-adapted population (> 100 generations on tomato plants, Table 2, Fig. 1c) did not significantly differ in their level of adaptation to bean than the stock population (Fig. 1f). This population performed equally well

on bean leaves compared with females from the stock population (Table 2).

Effects of dispersal and competition on longevity

For all populations, longevity was only impacted by plant type, with higher mortality on tomato than on bean (Table 3, Table S2, Fig. 2).

Fecundity–longevity trade-off

Female mites show a nonlinear relationship between fecundity and longevity for both generations and on both host plants (Table 4, Fig. 3). For both generations, only host plant has a significant effect on the fecundity–longevity relationship (Table 4, Table S3). There is an optimal longevity for which females have the maximum fecundity, and a further increase in longevity results does not result in a further increase (Fig. 3).

Adaptation to tomato in the experimental plants (before removal of juvenile and maternal effects)

For both generations, population sizes on the complete tomato plants were only affected by the competition treatment ($F_{1,54} = 94.18$, $P < 0.0001$, $R^2 = 0.64$ and $F_{1,54} = 169.7$, $P < 0.0001$, $R^2 = 0.76$ for generations 9 and 12, respectively). Populations under competition were more likely to have small population sizes than populations without competition (Fig. 4a,b) ($t = -9.71$, $P < 0.0001$; $t = -13.03$, $P < 0.0001$ for generations 9 and 12, respectively). Furthermore, populations with competition experienced more extinction events ($Z = 7.32$, $P < 0.0001$, Fig. 4c) and were less likely to survive ($Z = -2.301$, $P = 0.021$, Fig. 4d) than populations without competition. However, an increase in immigration reduces the number of extinction events

Table 1 Summary of final mixed models explaining total fecundity for female mites from populations evolving on tomato plants after eight and 20 generations. After eight generations, dispersal does not have a significant effect on adaptation to tomato. For this generation, we could only sample females from populations without competition. After 20 generations, there is a significant interaction between dispersal and competition. Whereas an increase of dispersal significantly decreases fecundity for populations without competition, dispersal does not have a strong effect for populations with competition.

	Coefficient	Estimate	SE	z value	P
Generation 8 no competition	Intercept	2.43	0.12	19.54	< 0.0001
Generation 20 Full Factorial Model	Intercept (no competition, 10 mites/week)	1.21	0.51	2.37	0.018
	Competition	1.64	0.63	2.61	0.009
	Dispersal (5 mites per week)	1.26	0.63	2.00	0.046
	Dispersal (3 mites per week)	1.83	0.58	3.15	0.002
	Dispersal (2 mites per week)	1.77	0.60	2.94	0.003
	Competition × Dispersal (5 mites per week)	−2.11	0.90	−2.35	0.019
	Competition × Dispersal (3 mites per week)	−2.53	0.97	−2.60	0.009
	Competition × Dispersal (2 mites per week)	−1.86	0.84	−2.22	0.027
	Intercept (2 mites per week)	2.99	0.23	13.02	< 0.0001
Generation 20 no competition	Dispersal (3 mites per week)	0.07	0.30	0.23	0.817
	Dispersal (5 mites per week)	−0.52	0.36	−1.47	0.140
	Dispersal (10 mites per week)	−1.68	0.45	−3.75	0.0002

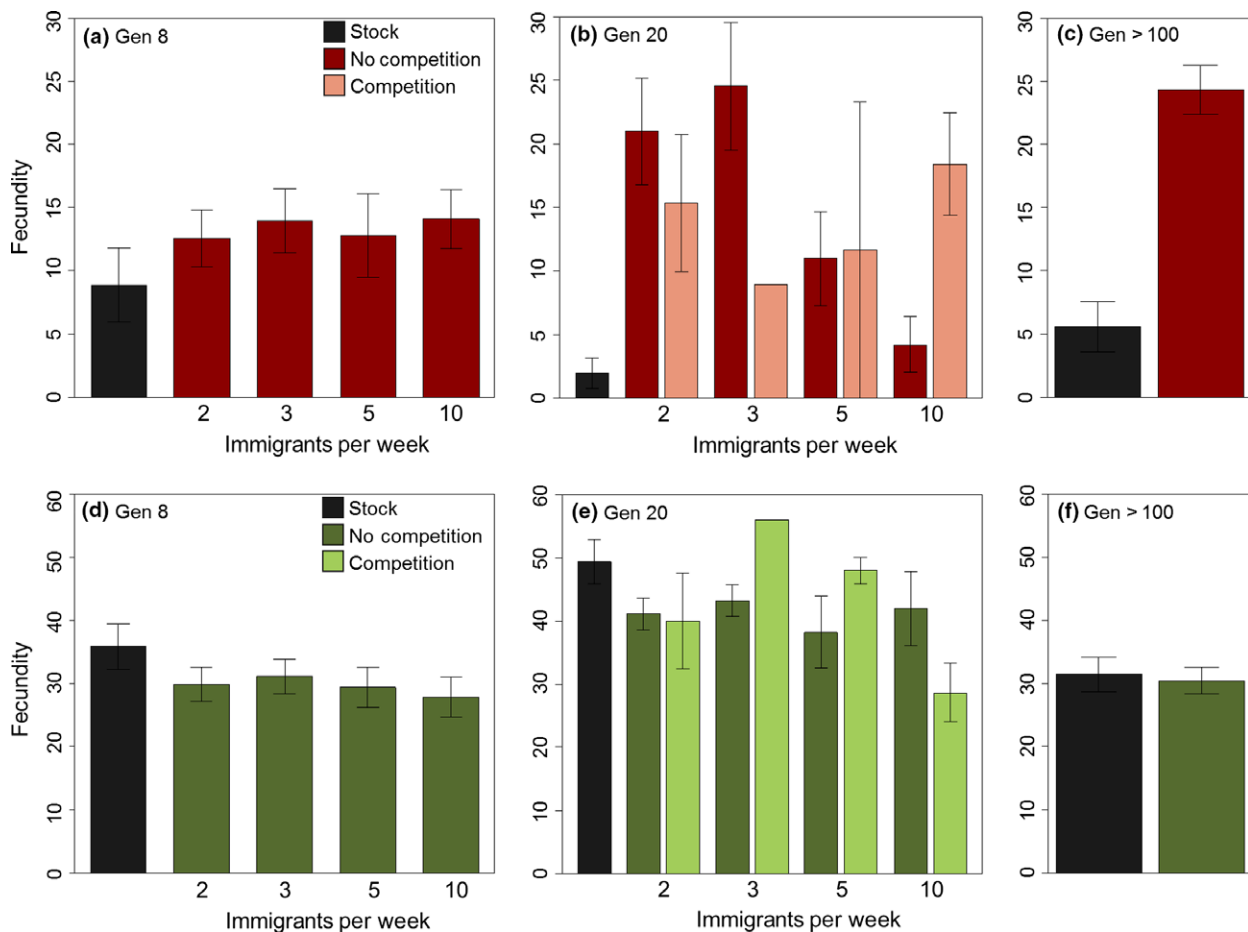


Fig. 1 Fecundity on tomato (red) and on bean (green) plants of female mites evolving on tomato plants: (a, d) populations without competition after eight generations on tomato plants under four levels of dispersal, (b, e) populations with and without interspecific competition (with *Tetranychus evansi*) after 20 generations on tomato plants under four levels of dispersal and (c, f) population without competition adapted to tomato plants for more than 100 generations. Fecundity of the stock population is plotted in black. Number of females used for the plots: (a) 10, 17, 17, 9, 15; (b) 4, 4, 3, 9, 1, 5, 3, 4, 5; (c) 16, 28; (d) 10, 16, 20, 12, 15; (e) 5, 7, 3, 8, 1, 4, 3, 4, 8; (f) 17, 27.

in populations with competition ($Z = -3.56$, $P = 0.0004$, Fig. 4c) and increases population survival ($Z = 2.053$, $P = 0.040$, Fig. 4d). See Table S4 for model selection.

Discussion

Our study shows that competition counteracts the negative effect that dispersal exerts on adaptation. Populations with competition that weekly received the highest number of immigrants (10 mites per week) had significantly higher fecundity than populations without competition from the same dispersal level. Competition might help adaptation under high dispersal levels possibly by exerting stronger selection on the population, which might increase mortality of newly arrived immigrants before mating with the local population.

Even though populations under competition are able to adapt to tomato plants, our results show that interspecific competition had a strong negative effect on population size and extinction risk in the experimental populations (in the experimental plants, before removing maternal and juvenile effects). The focal *T. urticae* mites have to cope with strong competition from *T. evansi*, which is a phylogenetically related competitor that is already adapted to tomato. This resulted in consistently smaller populations of *T. urticae* (Fig. S2) that were more prone to extinction than populations without competition. Because of higher extinction risk, populations were on average younger than populations without competition (9–12 generations on tomato for population with competition and the highest dispersal level vs. 19–20 generations for the most adapted population without competition). Although populations with

Table 2 Adaptation to tomato was tested using multiple comparisons (HSD test) between experimental populations and the stock (no-adapted) population. Whereas no adaptation was observed after eight generations, adaptation to tomato was observed at generation 20 for several treatments. Cost of adaptation: the loss of adaptation to bean plants after been under selection on tomato plants was tested using multiple comparisons (HSD test) between the fecundity of the experimental populations on bean plants against the fecundity of the stock population on bean plants. We did not observe a cost of adaptation for neither generations or treatments.

	Comparison	Estimate	SE	z value	Pr(> z)
Adaptation to tomato					
Generation 8 no-competition tomato	2 mites per week – stock	0.39	0.58	0.68	0.96
	3 mites per week – stock	0.29	0.58	0.50	0.99
	5 mites per week – stock	0.05	0.60	0.09	1.00
	10 mites per week – stock	0.25	0.58	0.43	0.99
Generation 20 no-competition tomato	2 mites per week – stock	2.34	0.54	4.33	< 0.001
	3 mites per week – stock	2.41	0.53	4.57	< 0.001
	5 mites per week – stock	1.80	0.56	3.25	0.01
	10 mites per week – stock	0.94	0.62	1.52	0.53
Generation 20 competition tomato	2 mites per week – stock	2.10	0.47	4.48	0.00
	10 mites per week – stock	2.20	0.45	4.91	0.00
Generation > 100 tomato	Adapted – stock	1.47	0.14	10.37	< 0.001
Cost of adaptation					
Generation 8 no-competition bean	2 mites per week – stock	–0.23	0.22	–1.03	0.834
	3 mites per week – stock	–0.12	0.22	–0.57	0.979
	5 mites per week – stock	–0.20	0.22	–0.89	0.898
	10 mites per week – stock	–0.32	0.22	–1.45	0.582
Generation 20 no-competition bean	2 mites per week – stock	–0.18	0.09	–2.11	0.213
	3 mites per week – stock	–0.13	0.08	–1.60	0.496
	5 mites per week – stock	–0.26	0.10	–2.49	0.092
	10 mites per week – stock	–0.16	0.10	–1.62	0.479
Generation 20 competition bean	2 mites per week – stock	–0.17	0.26	–0.64	0.918
	5 mites per week – stock	–0.04	0.26	–0.17	0.998
	10 mites per week – stock	–0.59	0.24	–2.39	0.078
Generation > 100 bean	Adapted – stock	0.05	0.10	–0.52	0.951

competition had less time to evolve, the stronger selection exerted by competition (that purges populations from maladapted individuals) might have allowed these populations to evolve faster.

The effect of *T. evansi* on *T. urticae* can be caused by simple resource competition. However, it might be more complex as both species are known to regulate tomato antiherbivory defences (Kant *et al.*, 2004, 2008; Sarmiento *et al.*, 2011a; Godinho *et al.*, 2015). *Tetranychus evansi* can down-regulate tomato defences, potentially favouring *T. urticae* (Sarmiento *et al.*, 2011a; Godinho *et al.*, 2015). However, it has been shown that *T. urticae* cannot benefit from this down-regulation because of the silken webs *T. evansi* produces, which makes it difficult to reach the leaves to feed on Ref. (Sarmiento *et al.*, 2011b). Furthermore, *T. evansi* can outcompete *T. urticae* by exerting a strong reproductive interference (Sato *et al.*, 2014). The possible positive effects of *T. evansi* on *T. urticae* are, therefore, outnumbered by negative direct effects via exploitative and interference competition and reproductive interference.

Our study shows that dispersal plays an important role in the adaptation process of *T. urticae* to tomato and that its effects depend on the biological interactions derived from the community context. An increase in

Table 3 Female mites were more likely to die on tomato plants than on bean plants, regardless generation and treatment combination. Summary of the survival analysis using a cox proportional hazard mixed effects models.

	Effect	Coefficient	exp (coef)	SE (coef)	z	P
Generation 8 and 20 no competition	Tomato	0.72	2.06	0.19	3.7	0.0002
Generation 20	Tomato	1.26	3.54	0.32	3.9	< 0.0001

dispersal negatively affects the adaptation to tomato of populations without competition. However, dispersal can have a positive effect for populations that co-occur with a competitor. We show that dispersal can reduce extinction risk of populations with competition, which allow them to persist long enough to start the adaptation process. In the competition treatment, however, longer persistence of populations did not result in higher levels of adaptation, but compared to situations without competition that experienced genetic load (thus lower fitness), fitness in populations with competition is maintained. Although less extinction, due to a

Fig. 2 Survival curves for female longevity: (a) on tomato leaves and (b) on bean leaves. For both generations (G) 8 and 20 and competition treatments (nc: no competition, c: competition).

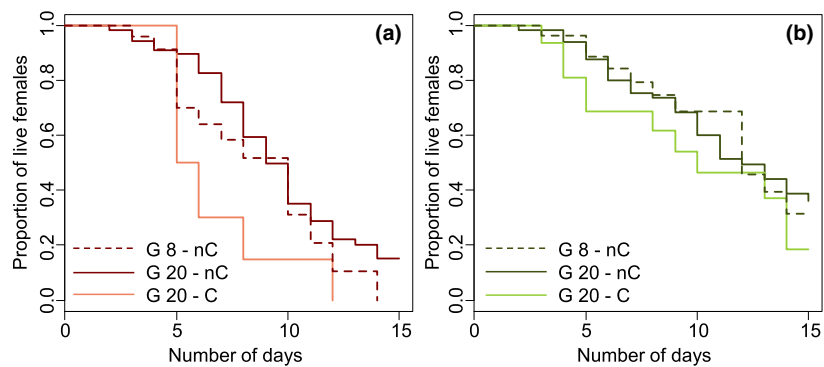


Table 4 Summary of best linear mixed model explaining the relationship between longevity and fecundity of female mites for generations 8 and 20. There is a quadratic relationship between both traits for both generations and plant species. There is an optimal value of longevity for which fecundity is maximum.

	Coefficient	Estimate	SE	d.f.	<i>t</i>	<i>P</i>
Generation 8	Intercept	−19.60	7.54	66	−2.60	0.01
	Bean	16.45	2.02	66	8.14	0.00
	Longevity	6.91	1.82	66	3.79	0.00
	Longevity ²	−0.33	0.10	66	−3.16	0.00
Generation 20	Intercept	−18.20	9.50	26	−1.92	0.07
	Bean	19.17	2.89	26	6.64	0.00
	Longevity	7.82	2.55	26	3.06	0.01
	Longevity ²	−0.35	0.15	26	−2.39	0.02

higher influx of immigrants, could also mean a greater evolutionary potential, we showed for populations without competition that an increase of dispersal has a negative effect on adaptation (presumably due to genetic load). We find that this negative effect is counteracted by competition and suggest that this is because interspecific competition exerts a stronger selection pressure on both immigrants and the resident populations, purging them from maladapted individuals. A higher selection on immigrants might entail a reduction of genetic load, and hence, the effective number of immigrants for the highest dispersal level under competition might be comparable to a lower dispersal level without competition. Alternatively, a higher selection on the resident population might imply a reduction of population size and hence greater opportunity for demographic or evolutionary rescue. A low number of immigrants under competition could lead to a lower fecundity if there is not enough genetic variation in the population. However, our results show, for both competition and the noncompetition treatments, that receiving a low number of immigrants does not negatively affect adaptation.

Potential mechanisms for the positive and negative effects of dispersal on adaptation can be the following: (i) genetic and demographic rescue or reinforcement

and (ii) genetic load or fitness decrease due to exceeding the carrying capacity (Garant *et al.*, 2007), respectively. Genetic and demographic rescue is particularly important for small populations with a very low influx of immigrants or for populations coping with competition. Dispersal can introduce alleles that bring a fitness advantage in the new habitat, and it can increase population sizes, counteracting the negative demographic effects of competition. Reinforcement, the evolution of premating isolation by selection against hybrids or locally maladapted genotypes, can act through mechanisms such as habitat choice or mate choice (Lenormand, 2012). In walking stick insects, discrimination against mates from other populations has been shown to be greater when migration rates are high enough for reinforcement to evolve, but low enough to prevent adaptive divergence due to genetic load, for example at intermediate dispersal rates (Nosil *et al.*, 2003). In *T. urticae*, discrimination against immigrants has been reported as well: males adapted to tomato plants prefer females from the same strain over females from a cucumber-adapted strain (Gotoh *et al.*, 1993). However, females adapted to tomato plants do not show a preference for males coming from different host plants (Magalhaes *et al.*, 2009). The positive effects of dispersal on spider mites' adaptation can be through both genetic/demographic rescue and reinforcement. Hence, our study is a first step in understanding the relative importance of these two mechanisms for local adaptation in experimental and natural conditions.

The observed negative effects of dispersal on adaptation to tomato are more likely due to genetic load rather than due to overall fitness reduction as a result of surpassing carrying capacity. Populations with high dispersal levels have a large proportion of immigrants coming from the stock population, which increases the chances of gene swamping. However, newly arrived immigrants (from the stock population) might carry over fitness benefits from having been on bean. We have shown that females from the stock population (after common garden to remove juvenile and maternal effects) perform poorly on tomato plants in comparison with females from the experimental populations that

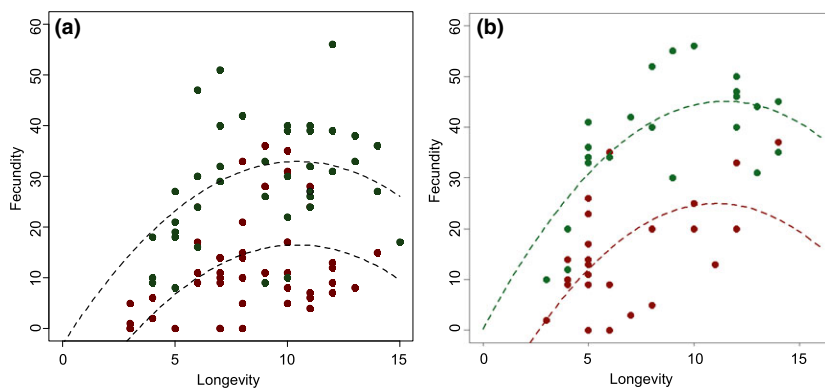


Fig. 3 There is a quadratic relationship between fecundity and longevity for both generations 8 (a) and 20 (b), regardless of plant species, indicating an optimal value of longevity where fecundity is maximal.

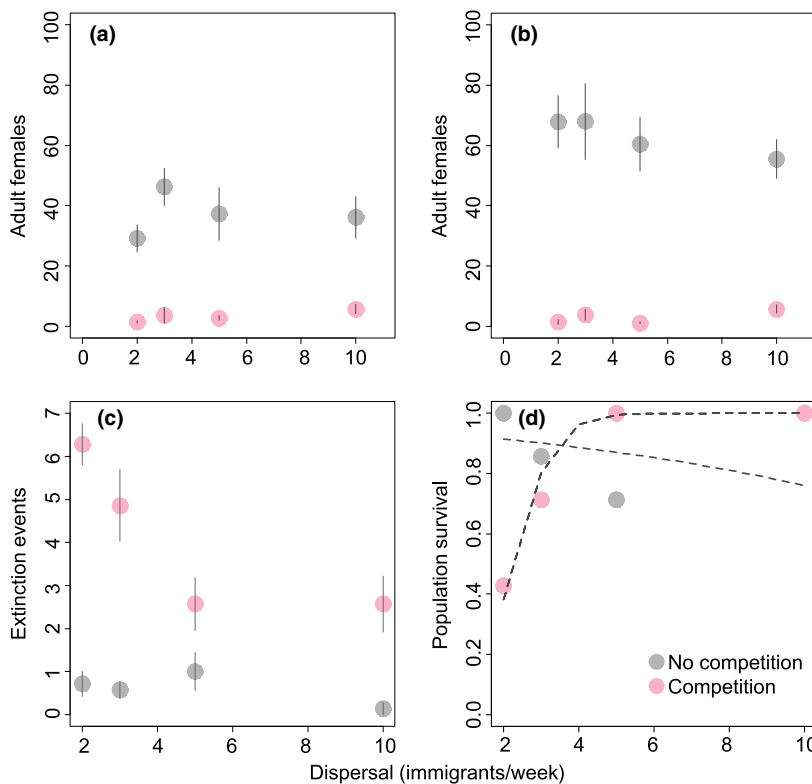


Fig. 4 Effect of dispersal and interspecific competition on population size (number of adult females) at generations 9 (a) and 12 (b), on the number of extinction events until generation 12 (c) and on population survival at generation 20 (d). Populations with interspecific competition are smaller and at higher risk of extinction than populations without competition. A higher influx of immigrants increases survival and reduces the number of extinction events of populations with interspecific competition. The fitted lines in (c) were estimated with a generalized linear model using a binomial error distribution.

have been selected on tomato plants (except the population without competition and the highest level of dispersal). Although we cannot discard that those populations might carry over some fitness benefits via epigenetics, population size data of the beginning of our evolutionary experiment (1 week, < 1 generation) suggest that females coming from the stock population suffer high mortality on the new tomato plants (Fig. S1). Additionally, it is unlikely that dispersal has a significant effect on intraspecific competition, because population sizes of the experimental populations without competition (which were always larger than

populations with competition and thus more prone to suffer from intraspecific competition) did not significantly increase with an increase in dispersal for either generation 9 or 12.

The adaptation to tomato in the two-spotted spider mite was driven by an increase in fecundity, but not in female longevity. This finding is in line with previous studies that showed that in spite of the genetic variation in both life-history traits, fecundity increases under selection whereas longevity remains unchanged (Magalhaes *et al.*, 2007). Adaptation was not accompanied by a cost on the ancestral host or by variation in

trade-offs between life-history traits. There is, however, a quadratic relationship between longevity and fecundity for both generations 8 and 20. There is an optimal value of longevity for which fecundity is maximum. Longevity has been shown to be a trait that does not evolve after selection (Magalhaes *et al.*, 2007), and our results suggest that this might be related to the specific relationship between fecundity and longevity: a trade-off between both traits when surpassing the optimal longevity value. If an increase of this trait is linked to a reduction of fecundity, evolution of longevity might not occur.

Lack of adaptation costs have been shown in most previous studies (Van Leeuwen *et al.*, 2008; Magalhaes *et al.*, 2009; Tien *et al.*, 2010). Although some studies reported costs of adaptation (Gould, 1979; Fry, 1990; Agrawal, 2000), the validity of their results has been questioned (Magalhaes *et al.*, 2009). Our results showed that adaptation does not bring costs; mites from the different selection regimes performed as well on the ancestral host plant as females coming from the population kept in the ancestral host.

It is unlikely that the lack of cost of adaptation is the result of the constant influx of immigrants from the ancestral bean host that frequently brings bean-adapted genes, because the population adapted to tomato for more than 100 generations that never received any influx of immigrants did not show any cost on the ancestral bean host: it still performed as well as the stock population. A more plausible reason for the lack of adaptation costs is that mites coming from the tomato selection regime, which are able to deal with the antiherbivore defences of tomato plants, can still easily deal with defences of bean plants. Because bean plants are a highly suitable host, tomato-adapted mites do not need special physiological changes to digest and cope with its antiherbivory defences. An analogous situation has been reported in mites selected for pesticide resistance: mites adapted to pesticides do not show fitness costs when they are not exposed to pesticide (Van Leeuwen *et al.*, 2008). An interesting question is whether costs of adaptation are generally not present in this species or whether its detection depends upon the plant species used in experiments; costs might not be detectable under optimal conditions, for example low population densities, optimal temperatures and low-toxicity host plants. However, the fact that not all mite species are generalist must indicate some cost.

Our results shed light on how fast species adapt to novel habitats under different scenarios of habitat connectivity (different levels of dispersal) and competition. We show that dispersal exerts a negative effect on adaptation in a scenario without competition. Competition exerts stronger selection on populations, which on the one hand reduces population sizes and increases extinction risk, but on the other hand may favour rapid evolution. In the face of the current rapid habitat

changes that lead to species failing to keep pace with these changes eventually putting them in risk of extinction, we need to consider both the community context and the habitat connectivity when studying local adaptation and the potential of species to adapt to environmental change.

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Author's contributions

AA, RSE and DB developed the study idea; AA, RSE and DB designed the experiment; AA and KB performed the experiments; AA collated the data and performed the statistical analyses; AA wrote the first draft of the manuscript, and all authors contributed to discussions and revisions.

Conflict of interest

None of the authors have competing interests.

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Supporting information

Additional Supporting Information may be found online in the supporting information tab for this article: **Table S1** Fecundity. For model selection, we performed a backward step-wise removal of non-significant effects (> 0.05), starting with the interaction terms.

Table S2 Survival analysis: Model selection was performed using a backward step-wise removal of non-significant effects (> 0.05), starting with the interaction terms.

Table S3 Model selection for fecundity – longevity tradeoffs.

Table S4 Model selection for the effect of competition and dispersal on population sizes (at generation 9 and 12), on the number of extinction events (during 12 generations) and population survival (at generation 20) on complete tomato plants (before removal of epigenetic effects).

Figure S1 Proportion of death females at the beginning of the evolutionary experiment (6 days after the first immigration routine).

Figure S2 Average *T. urticae* population sizes (number of adult females) during the first 12.5 generations on tomato plants.

Data deposited at Dryad: <https://doi.org/10.5061/dryad.486g4>

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